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ORIGINAL ARTICLE

Importance of bird seed dispersal in the development of characteristic vegetation on termite mounds in north-eastern Namibia

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ABSTRACT Mound-building termites function as ecological engineers in tropical savanna landscapes. Large termite mounds support a greater diversity of plants than off-mound areas, but little is known about the process by which diverse mound vegetation develops. This study examined the dispersal mode of woody plants on termite mounds and assessed the process of plant assemblage formation on mounds. This study focused on mound status (termites active *vs.* inactive) and mound microtopography (mound cones *vs.* pediments) to develop a chronology of vegetation development. The frequencies of occurrence of woody plants were lower on active mounds (67%), especially on cones (46%) compared to inactive mounds (95%). Species richness and the abundance of woody plants increased in the order of cones, pediments of active mounds and inactive mounds. The proportion of bird-dispersed plant species was much higher on mounds (＞40%) than in off-mound areas (3%). *Salvadora persica* was the main bird-dispersed plant and occurred preferentially on active mounds. A schematic plant succession model incorporating the process of endozoochory was developed to explain vegetation development on active mounds.

Key words: Mopane woodland, *Salvadora persica*, savanna, seed dispersal

INTRODUCTION

Termites have major effects on savanna landscapes, where they function as ecosystem engineers (Dangerfield et al. 1998, Jouquet et al. 2011). Termite mounds support more diverse woody plant assemblages (Loveridge and Moe 2004, Traore et al. 2008) and herbaceous layers (Moe et al. 2009, Okullo and Moe 2012a, b) than surrounding tracts of savanna. Termite-induced resource heterogeneity, such as soil composition (Sileshi et al. 2010, Erpenbach et al. 2013) and soil moisture (Dangerfield et al. 1998, Konate et al. 1999), induces this vegetation pattern. Spatial heterogeneity is also a factor, in that termite mounds act as refugia for plants from fire (Moe et al. 2009, Joseph et al. 2013) and flooding (McCarthy et al. 1998, Bloesch 2008). Okullo et al. (2012a) suggested that large herbivores maintain termite-induced differences in savanna vegetation.

Although there are indications that animal seed dispersal contributes to the formation of diverse plant assemblages on mounds (McCarthy et al. 1998), the dispersal modes of the plants on mounds have not been evaluated in detail. Therefore, this study examined the dispersal modes of the vegetation on termite mounds, compared with the surrounding vegetation, and assessed the process of vegetation development on mounds using data on the dispersal mode. The development processes of mound vegetation remain largely unexplored because of the difficulty in determining the age of mounds and compiling relevant data over protracted periods. To this end, this study focused on mound status (termites active or not) and topographic structures within mounds (mound cone *vs.* mound pediment). Mound status and size were used as indicators of chronology.

MATERIALS AND METHODS

Research site

The research site was located within the Muyako Community Forest (17.88°S, 24.40°E; Fig. 1) in the Zambezi region of Namibia (formerly the Caprivi region). The forest was assigned CF status in 2008. Approximately 1,800 people live within this 12,000-ha tract.

The study site is at an altitude of 1000 m, and the topography is nearly flat. The annual precipitation is ＞ 650 mm (Mendelsohn et al. 2002), with most rain falling between October and March. The average temperature is 20-22℃. September is the warmest month (range 14.1-33.8℃) and June is the coolest (range 6.1-24.5℃)

(Namibia Meteorological Service 2013). Large areas of the landscape are covered by Kalahari sand (Mendelsohn et al. 2002). The research site lay between the Zambezi River to the north and the Chobe River, downstream from the Kwando River, to the south. The site was located on the boundary between the Kwando and Zambezi drainage basins; some areas were inundated during the rainy season. Lyambezi Lake, which contained water year-round, lay to the west of the study site (Fig. 1).

The local vegetation has been classified as mopane, *Colophospermum mopane* (J. Kirk ex Benth.) J. Kirk ex J. Léonard, woodland, *Acacia* woodlands, riparian forests and floodplains, which cover small areas of the landscape (Mendelsohn and Roberts 1997). This study focused on woody vegetation because the understorey vegetation of mopane veldt, including grasses and herbs, is poorly developed (Werger and Coetzee 1978). The investigations were conducted in October-December 2009, June, July and December 2010 and November 2012.

Termite mounds

Termite mounds are distributed widely throughout this area, except at Lyambezi Lake (Fig. 1). Seventy termite mounds wider than 1 m in diameter were selected based on accessibility and investigated in detail. Anthropogenically impacted mounds and vegetation were excluded. In this area, people use the soil of active termite mounds and woody plants as building materials. The 70 mounds used in this study were classified after rainfall in 2009 as either active or inactive (as indicated by signs of new construction on the mounds or the presence of termites). New construction is necessary as mounds age or become damaged, usually immediately after rainfall. New structures are easily identifiable. Interiors of unidentified conical mounds were checked for the presence or absence of termites. The mounds included in this study were constructed by fungus-growing termites of the genus *Macrotermes* (Uys 2002).

To determine the relative ages of mounds, active mounds were classified based on the presence or absence of pediments surrounding conical parts, formed from the deposition of material freed by mound erosion (Fig. 2). Inactive mounds were not classified in this manner because the boundaries between cones and pediments were indistinct. In this study, the term “cone” was used to refer to both active mounds without pediments and the conical parts of active mounds with pediments.

Dangerfield et al. (1998) and McCarthy et al. (1998, 2012) suggested that islands on the floodplain of the Okavango Delta originated as mounds built by *Macrotermes michaelseni* (Sjöstedt), with subsequent expansion of the original structures through accumulation of minerals in groundwater (as a result of transpiration in plants growing on the mounds). They also suggested that islands in the Okavango Delta developed through repeated colonisation of *Macrotermes* mounds. At the Namibian study site, half of the active mounds had pediments surrounding the conical central parts (Fig. 2 (i)); similar structures occurred on some inactive mounds. After classification, large, inactive mounds were therefore treated as structures that had developed sequentially from conical, active mounds. Mound classification into categories of active or inactive, and active with or without pediments, provided guidelines for determining mound chronology and whether a mound was new or old with respect to its vegetation development process; a mound was classified as new if active without pediments, older if active with pediments and oldest if large and inactive.

Vegetation survey

To compare vegetation between active and inactive mounds, species richness and the abundance of mature woody plants (height ≥ 1.3 m and diameter at breast height ≥ 1 cm) were recorded on the 70 mounds. The distance between mounds was 13 m or more. Thirteen comparison quadrats were set in off-mound areas (each 20 × 20 m), and the mature woody plants were recorded (Fig. 1). The quadrats were located in the savanna at least 50 m from the mound peripheries and outside a human residential area.

To determine the sequential trends in woody plant spatial distributions from the mounds outward, the taxonomic composition and abundance of woody species were surveyed along two belt transects (each 50 m long and 2 m wide) laid out from the tops of an active A and an inactive B mound. The surveyed trees were classified into mature trees, saplings (0.3 m≤ height＜1.3 m) and seedlings (height＜0.3 m). Topographic structure along transects was surveyed using a hand-level and a tape measure, and the positions of all woody plants were plotted on the transect profiles. Mounds A and B were not included in the 70 mounds selected previously. This survey was conducted in November 2009 at the beginning of the rainy season.

Plant species were identified by the author using leaves, as well as flowers and fruit if present, using van Wyk and van Wyk (1997) and Smith and van Wyk (2009). The plant species nomenclature followed the African Plant Database (2013).

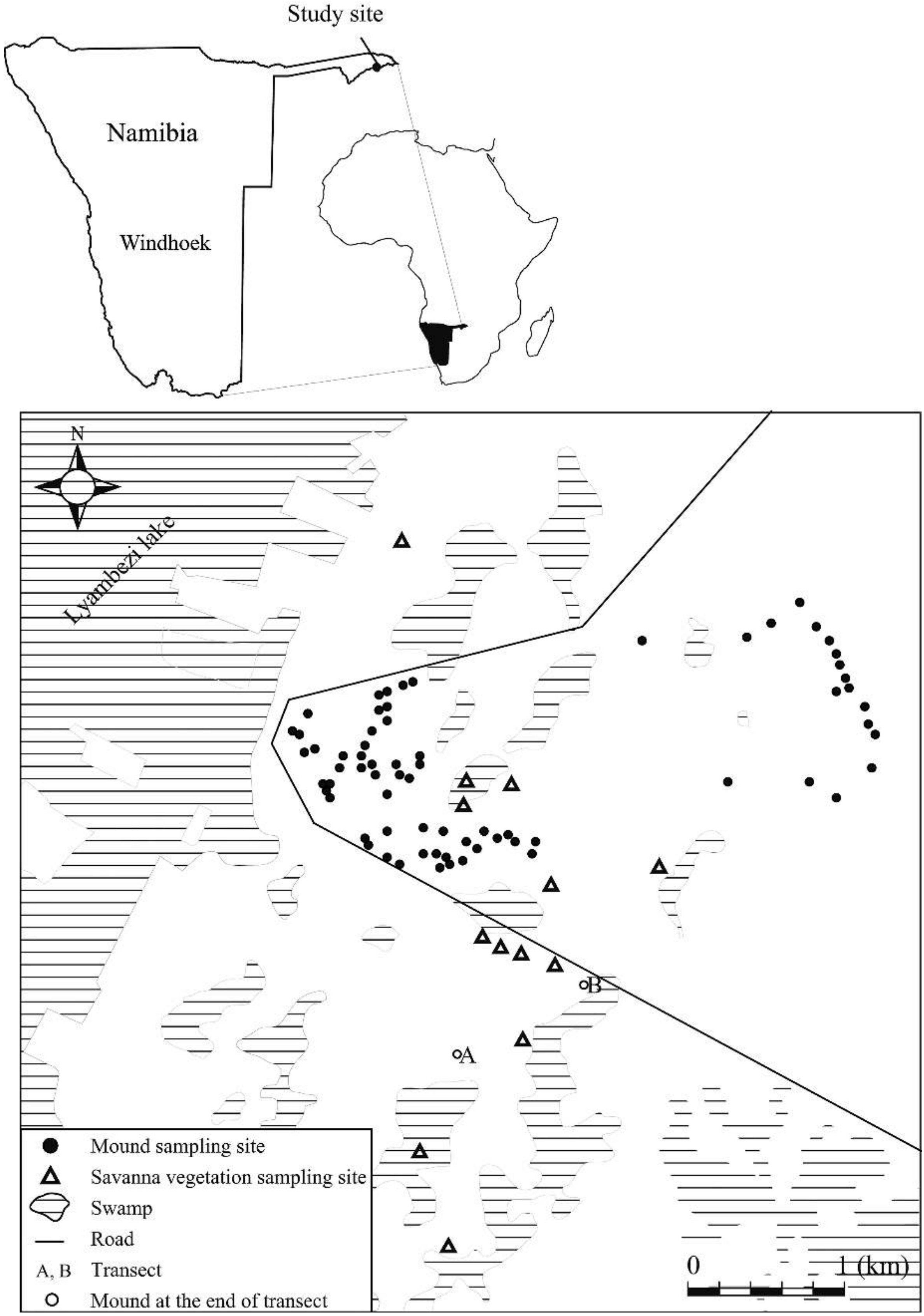

Fig. 1. Study site in Muyako CF, Namibia. Apart from the permanent water body of Lyambezi Lake, damp habitats during the dry season were present only in small swamps. Termite mounds are distributed widely throughout this area, except at Lyambezi Lake.

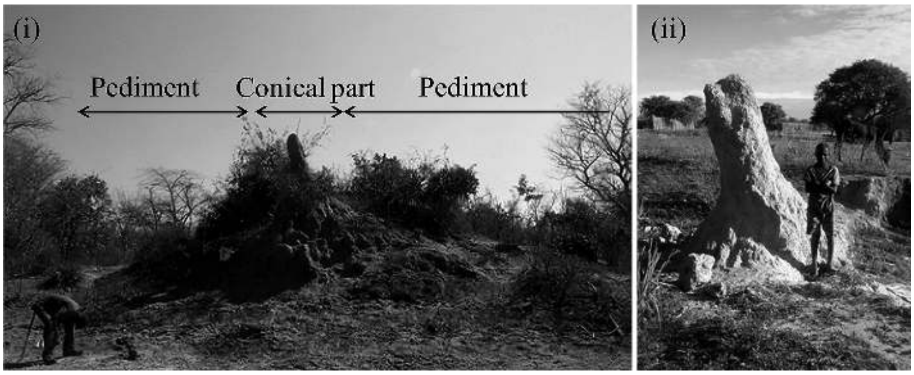

Fig. 2. Active mounds with (i) and without (ii) pediments in north-eastern Namibia.

Seed dispersal mode and seed dispersers

For consideration of the mechanisms by which plants disperse among mounds, preliminary field observations were conducted on seed dispersal vectors of *Salvadora persica* L., which has fresh red fruits 5 mm in diameter. A *S. persica* tree with many fruit was selected for observation. The seed and fruit handling behaviours of animal species were observed for 2 days in November 2012 during the following periods: 0600–1400 and 1000–1800 (for a total of 16 h). The abundances, species identities and behaviours of visiting animals were recorded. Bird species were identified by the author, using Sinclair and Ryan (2009); the nomenclature followed Avibase, the World Bird Database (2013).

Additionally, seeds in animal droppings were observed in the field in December 2010. The literature was consulted to determine species (Timberlake 1995,Wunderle 1997, McCarthy et al. 1998, Dean et al. 1999, Hovestadt et al. 1999, Dudley 2000, Sidibe et al. 2002, Smith and van Wyk 2009, Kirchmair et al. 2012). The dispersal agents of tree seeds were classified as birds, other vertebrates or wind.

Data analysis

The mound heights and diameters of active mounds with and without pediments and of inactive mounds were analysed using one-way analysis of variance (ANOVA) followed by multiple comparison tests (Tukey's HSD). Tree abundances and species richnesses among site types were compared using nonparametric Steel-Dwass multiple comparison tests after the Kruskal-Wallis test since discrete measures were analysed. The proportions of bird dispersed species and other dispersal modes, including other vertebrates and wind-dispersed species, were analysed using pairwise comparisons (with the Bonferroni adjusted p-value) among cones, pediments of active mounds, inactive mounds and off-mound areas, where the proportions of plant dispersal agents differed significantly ($p < 0.05$) using the χ^2 test.

To determine the relative effect of plot type (cone/pediment, active/inactive, on mound/off mound) on the abundance of each tree species, generalised linear models (GLMs) were constructed for the seven highest-ranked woody species; at least 40 individuals of each of these species were subjected to analysis. The GLM incorporated tree abundance as a response variable and plot type as an explanatory variable, with inclusion of the area of each plot as an offset factor. Poisson error distributions and logit link functions were applied, as provided in the GLM MASS package of R ver. 2.14.1 for Windows (R Foundation for Statistical Computing, Vienna, Austria). This analysis used pediment as a standard among the explanatory variables of the factor class; pediment appeared as the intercept in the results output. All statistical analyses were performed using R software (with $\alpha = 0.05$).

RESULTS

Vegetation on mounds

Active mounds without pediments were smaller in diameter than both active mounds with pediments ($p < 0.0001$) and inactive mounds ($p < 0.0001$; Table 1). Inactive mounds were shorter than active mounds with pediments ($p < 0.05$), while there were no significant differences in height between active mounds with and without pediments ($p = 0.05$) and between active mounds without pediments and inactive mounds ($p = 0.99$). No trees were present on 11 of 33 (33 %) active mounds (including 7 of 17 (41 %)

Table 1. Mound dimensions and abundances and species richnesses of woody plants (mean ± SD) on active mounds (with and without pediments) and inactive mounds in north-eastern Namibia. Total counts of woody plant individuals, woody plant species, and mounds without trees are provided for each category of mound

	Active mound		Inactive mound (n = 37)	ANOVA/Kruskal-Wallis	
	Without pediment (n = 17)	With pediment (n = 16)		F/ χ^2	p
Mound dimensions					
Height (m)	2.4 ± 1.0^{ab}	3.1 ± 1.0^{a}	2.4 ± 0.8^{b}	$F_{(2,67)} = 4.2$	< 0.05
Diameter (m)	2.7 ± 2.2^{a}	14.1 ± 5.6^{b}	16.9 ± 8.2^{b}	$F_{(2,67)} = 26.7$	< 0.0001
Total surveyed area (m^2)	155	2860	10157	−	−
Vegetation on mounds					
Tree numbers per mound	0.9 ± 1.1^{a}	4.6 ± 6.6^{a}	19.4 ± 18.8^{b}	$\chi^2_{(2)} = 29.1$	< 0.0001
Species richness per mound	0.6 ± 0.6^{a}	2.0 ± 1.8^{a}	4.4 ± 2.7^{b}	$\chi^2_{(2)} = 26.7$	< 0.0001
Total number of woody plants	15	75	712	−	−
Total number of woody plants species	4	13	20	−	−
Number of mounds without trees	7	4	2	−	−

* Different superscripted lowercase letters in rows indicate statistically significant differences among mound types ($p < 0.05$; Tukey's HSD for height and diameter or the Steel-Dwass test for tree numbers and species richness).

active mounds without pediments and 4 of 16 (25 %) with pediments) and 2 of 37 (5 %) inactive mounds (Table 1). Eighteen of 33 (54 %) active mounds had no trees on their cones. The species richness and abundance values of woody plants were higher on inactive mounds than on either active mounds with (species richness $p < 0.01$, abundance $p < 0.001$) or without pediments (both $p < 0.0001$; Table 1).

Thirty species of plants were encountered, and 12 of these were restricted to termite mounds; eight species occurred only in off-mound areas (Table 2). *Colophospermum mopane* occurred both on and off mounds, but not on the cones of active mounds. *Salvadora persica* was limited to mounds (Table 2). The occurrences of nonwoody plants, such as *Sansevieria pearsonii* N. E. Br. (Agavaceae) and *Aloe zebrina* Baker (Aloaceae), were strongly linked to mounds (Table 2); these plants were typically abundant in areas surrounding mounds.

Distributions of woody species on mounds

The occurrence of woody plants on active and inactive mounds differed among species (Fig. 3). On an active mound, mature specimens of the common species *C. mopane* and *Dichrostachys cinerea* (L.) Wight & Arn. (as well as their saplings and seedlings) occurred primarily on pediments and off-mound areas. Several tree species, including *S. persica*, *Commiphora glandulosa* Schinz, *Cordia* spp. and *Albizia anthelmintica* Brongn., occurred on the selected mound, and two (*S. persica* and *C. glandulosa*) occurred on the conical part (Fig. 3A). Distribution patterns were similar on an inactive mound; saplings of *Capparis tomentosa* Lam. grew with *S. persica* near the centre of this inactive mound (Fig. 3B).

Woody plant seed dispersal patterns on mounds

The proportions of woody plant dispersal modes differed among mound cones, pediments of active mounds, inactive mounds and off-mound areas ($\chi^2 = 329$, $p < 0.0001$, n = 1303; Fig. 4). Comparing the proportions of bird-dispersed species and other dispersal patterns, there were significant differences between mounds (cones, pediments of active mounds and inactive mounds) and off-mound areas (Table 3). The largest proportion of bird-dispersed trees included specimens of *S. persica*, which comprised 68 % of the total. This species was especially abundant on the cones of active mounds, followed by inactive mounds, compared with pediments of active mounds (Table 4). *Salvadora persica* comprised 64 % of the trees on cones. *Colophospermum mopane* was especially abundant on inactive mounds and in off-mound areas, and *D. cinerea* was also abundant at off-mound sites compared with pediments of inactive mounds (Table 4). *Terminalia prunioides* M. A. Lawson, *C. glandulosa* and *Euphorbia ingens* E. Mey. ex Boiss. were typically present on mounds (Table 2) and especially abundant on inactive mounds compared with active mound pediments (Table 4).

Table 2. Tree density per 100 m^2 (mean ± SD) on active/inactive mounds and in off-mound areas. Seed dispersal agents of each species in north-eastern Namibia are also provided

	Termite mounds				Off mound ($n_2 = 13$)	Dispersal agent
	Active			Inactive ($n_1 = 37$)		
	Without pediment ($n_1 = 17$)	With pediment ($n_1 = 16$)				
Plant species		Conial part	Pediment			
Colophospermum mopane	8.6 ± 19.6	0	<1	8.3 ± 26.9	6.2 ± 5.0	wind[8]
Salvadora persica	9.6 ± 19.2	4.9 ± 10.3	<1	3.4 ± 3.5	0	bird
Dichrostachys cinerea	0	0	<1	<1	2.1 ± 2.9	antelope/elephant[5, 10]
Terminalia prunioides	0	0	<1	<1	0	wind
Commiphora glandulosa	0	0	<1	<1	<1	bird
Rhus spp.	0	0	0	<1	<1	bird[5]
Euphorbia ingens	0	0	<1	1.3 ± 4.6	0	self/bird
Acacia nigrescens	0	0	<1	<1	<1	antelope[2]
Ximenia americana	0	0	0	<1	<1	primates[5]
Albizia anthelmintica	0	0	<1	<1	<1	antelope?
Combretum spp.	0	0	<1	<1	<1	wind[5]
Capparis tomentosa	<1	8.0 ± 31.8	<1	<1	<1	primates[5]
Acacia sp.	0	0	0	<1	<1	−
Commiphora mossambicensis	0	0	0	<1	0	bird
Fockea multiflora	0	0	<1	<1	0	wind
Acacia tortilis	0	0	0	0	<1	antelope[5]
Adansonia digitata	0	0	<1	<1	0	bird/mammal[3, 6, 10]
Cordia spp.	0	0	0	<1	0	bird/bats[9]
Garcinia livingstonei	0	0	0	<1	0	bird/mammal
Grewia spp.	0	0	0	0	<1	bird/mammal[2,5]
Ziziphus mucronata	0	0	0	0	<1	antelope/bird/elephant[2, 5]
Acacia melifera	0	0	0	0	<1	herbivore[1]
Berchemia discolor	0	0	0	0	<1	bird/mammal[2, 10]
Ehretia spp.	0	0	0	0	<1	bird[1]
Gymnosporia senegalensis	0	0	0	0	<1	animal[4]
Hyphaene petersiana	3.3 ± 13.7	0	0	0	0	elephant[10]
Lonchocarpus capassa	0	0	<1	0	0	antelope?[5]
Pilostigma thonningii	0	0	0	0	<1	mammal[3]
Sansevieria pearsonii	3/17	−	6/16	24/37	0	bird
Aloe zebrina	4/17	−	7/16	18/37	0	wind/bird[7]

* Average tree densities of less than one per 100 m^2 are indicated as <1.

** Frequencies per total sample area are indicated for *Sansevieria pearsonii* and *Aloe zebrina*.

*** The identities of plant seed dispersal agents were obtained from [1]Dean et al. (1999), [2]Dudley (2000), [3]Hovestadt et al. (1999), [4]Kirchmair et al. (2012), [5]McCarthy et al. (1998), [6]Sidibe et al. (2002), [7]Smith & Van Wyk (2009), [8]Timberlake (1995), [9]Wunderle (1997), [10]personal field observations of feeding behaviours on seeds and/or fruits or animal droppings; other dispersal agents were derived from dispersal syndromes (morphology of the seeds).

**** n_1: number of termite mounds, n_2: number of quadrats.

Observation of birds at *Salvadora persica*

In total, 2616 individual birds of 21 species were observed on a *S. persica* tree, and more than 98 % of these birds, 13 species, fed on the fruit (Table 5). The Wattled Starling *Creatophora cinerea* Meuschen accounted for 69 % of the total bird count, followed by Burchell's Starling *Lamprotornis australis* Smith, A., which comprised 13 % of the total.

DISCUSSION

This study's findings suggest that bird-dispersed

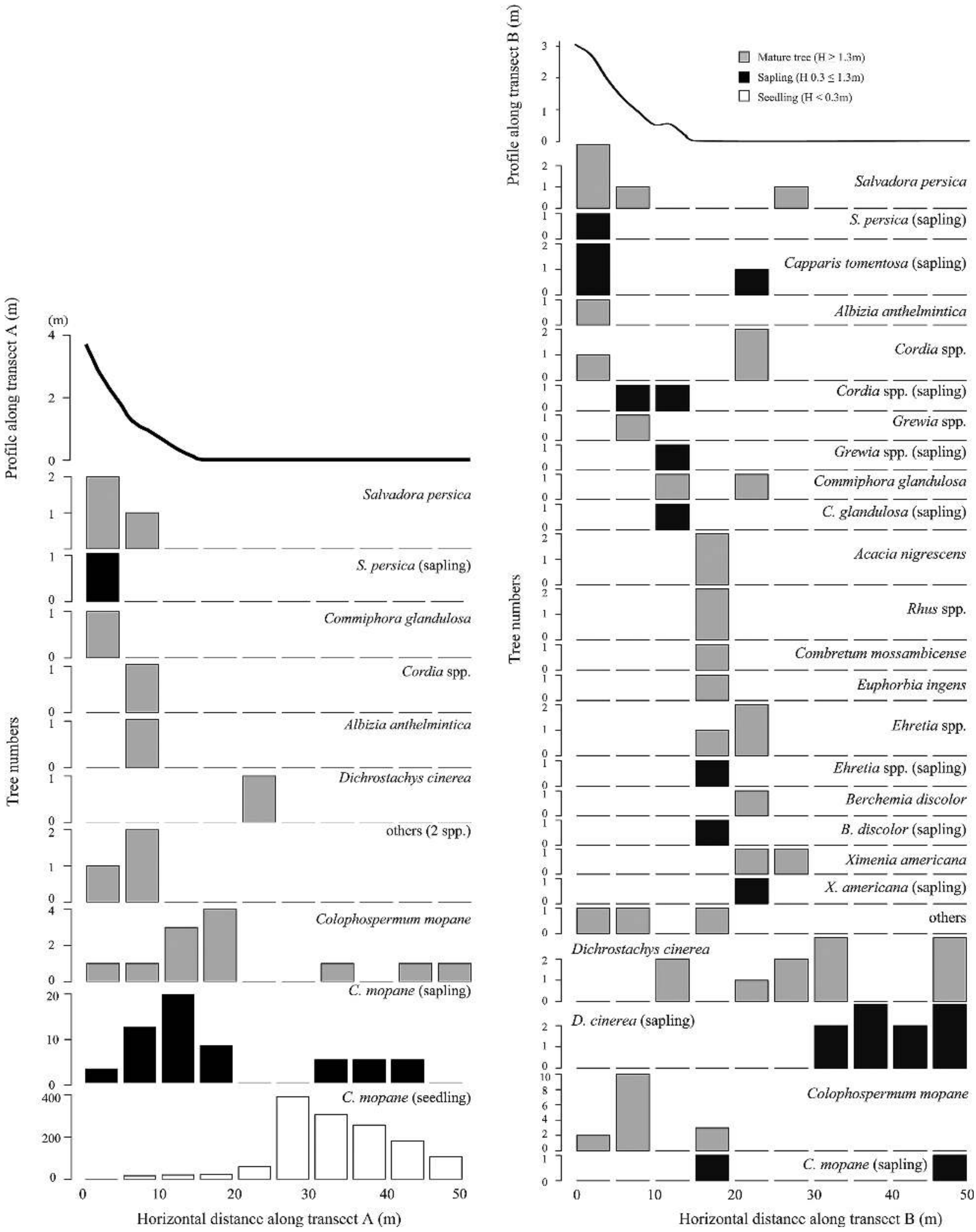

Fig. 3. Distributions of individual woody plant species on an active mound and in the surrounding savanna (A) as well as on an inactive mound and in the surrounding savanna (B). Line plots show the profiles of each transect, and bar-plots show the number of each woody plant species.

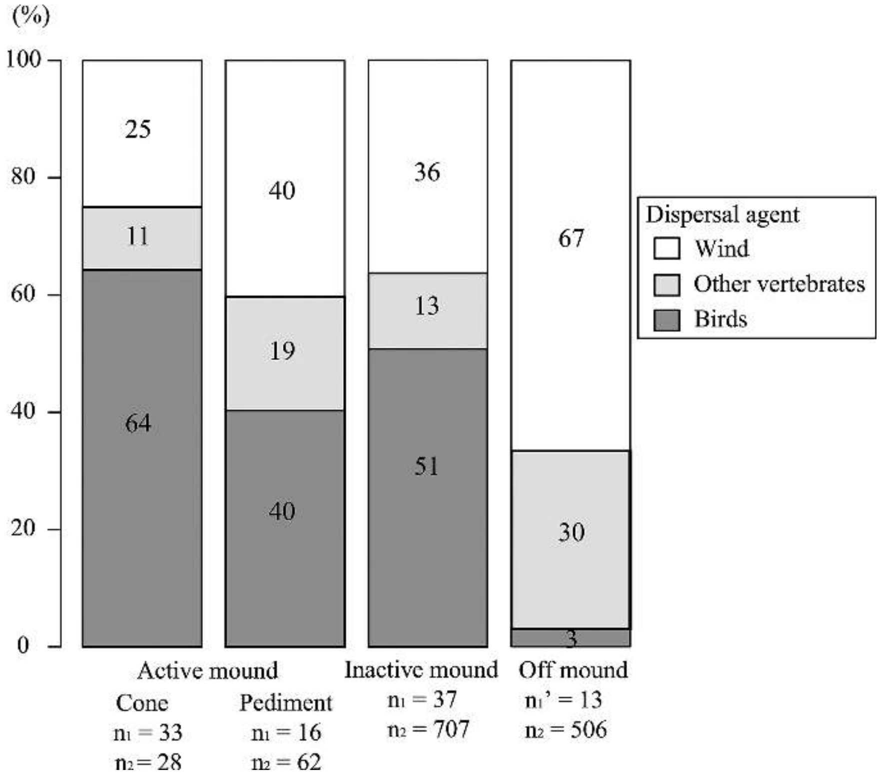

Fig. 4. The proportions of dispersal modes among woody plant species: bird dispersal, other animal(s) dispersal and wind dispersal. n_1: number of termite mounds, n_1': number of quadrats, n_2: number of trees.

Table 3. Results of pairwise tests (with the Bonferroni adjusted *p*-values) comparing the proportion of bird-dispersal and other dispersal modes among cones, pediments of acitve mounds, inactive mounds and off-mound areas

	Cone	Pediment	Inactive mound
Pediment	0.36	−	−
Inactive mound	1	0.89	−
Off mound area	$<$0.0001	$<$0.0001	$<$0.0001

species were much more abundant on mounds than in off-mound areas (Table 3). The observation of birds on *S. persica* and the features of the fruit suggested that the seeds are dispersed by birds. This species comprised the major proportion of bird-dispersed species (68 %) and was restricted to mounds (Table 2). Although 54 % of the active mound cones lacked trees, *S. persica* was more abundant on cones than on pediments or inactive mounds (Table 4) and comprised 64 % of the trees on cones. Many species of birds were observed feeding on the fruit of *S. persica*. Therefore, *S. persica* is a pioneer species on mounds, and bird dispersal might contribute to the restricted distribution of the trees.

In savanna landscapes, tree species with fleshy fruits generally have scattered distributions of mid- to large-sized individuals that are used by birds as nesting, resting and observation sites (Dean et al. 1999). Isolated trees in open areas act as perch sites, below which a heavy seed rain occurs in the birds' droppings, which in turn promote seedling establishment (Toh et al. 1999). Rocky outcrops also act as perches and have high densities of plants; such structures are called nurse rocks (Fuentes et al. 2001, Carlucci et al. 2011). Using information on plant dispersal in Brazil, Carlucci et al. (2011) suggested that perching of seed-dispersing bird species on rocks increases the local seed rain. Consequently, rocks act as nuclear foci of forest vegetation in the surrounding grassland. In addition, the effects of nonrandom faeces deposition by carnivores (*e.g.* open-site defaecation of civets (*Paradoxurus hermaphrodites*) in Malaysia (Nakashima et al. 2010) and maned wolf (*Chrysocyon brachyurus*) defaecation on termite mounds in Brazil (Dietz 1984)) have not been adequately investigated in north-eastern Namibia, where the genet (*Genetta* spp.) and jackal (*Canis* spp.) are common. Consequently, *S. persica* is probably preferentially dispersed to mounds by birds and other animals in the sparse mopane woodland, where the conical structures of termite mounds may well function as bird perches.

Colophospermum mopane and *Hyphaene petersiana* Klotzsch ex Mart., which grew on mound cones (Table 2), were probably exceptions to this bird-dispersal hypothesis

Table 4. Results of generalised linear models (GLMs) explaining the effect of plot type (cone/pediment/inactive mound/off mound) on tree abundance. Seven separate GLMs were constructed for the seven highest ranked woody species of which at least 40 individuals were present

Plant species	Variable	Coefficient	SE	Wald	df	P
Colophospermum mopane	Intercept	− 4.78	0.213	− 22.4	15	<0.0001
	Cone	0.776	0.434	1.79	32	0.074
	Off mound	2	0.22	9.08	12	<0.0001
	Inactive	0.799	0.225	3.55	36	<0.001
	Residual deviance	645				
Salvadora persica	Intercept	− 4.83	0.218	− 22.1	15	<0.0001
	Cone	1.77	0.321	5.5	32	<0.0001
	Off mound	− 18.5	962	− 0.019	12	0.99
	Inactive	1.1	0.228	4.82	36	<0.0001
	Residual deviance	299				
Dichrostachys cinerea	Intercept	− 6.78	0.577	− 11.7	15	<0.0001
	Cone	− 13.2	681	− 0.019	32	0.99
	Off mound	2.89	0.585	4.94	12	<0.0001
	Inactive	0.685	0.614	1.12	36	0.26
	Residual deviance	275				
Terminalia prunioides	Intercept	− 7.87	1	− 7.87	15	<0.0001
	Cone	− 13.1	1120	− 0.012	32	0.99
	Off mound	− 17.4	2610	− 0.007	12	0.99
	Inactive	2.76	1.01	2.74	36	<0.01
	Residual deviance	285				
Commiphora glandulosa	Intercept	− 7.18	0.707	− 10.2	15	<0.0001
	Cone	− 13.8	1120	− 0.012	32	0.99
	Off mound	− 0.682	1	− 0.682	12	0.5
	Inactive	1.67	0.724	2.31	36	<0.05
	Residual deviance	105				
Rhus spp.	Intercept	− 24.1	1990	− 0.012	15	0.99
	Cone	3.06	2281	0.001	32	1
	Off mound	18	1990	0.009	12	0.99
	Inactive	18.2	1990	0.009	36	0.99
	Residual deviance	167				
Euphorbia ingens	Intercept	− 7.18	0.707	− 10.2	15	<0.0001
	Cone	− 14.8	1850	− 0.008	32	0.99
	Off mound	− 19.1	4310	− 0.004	12	1
	Inactive	1.59	0.726	2.2	36	<0.05
	Residual deviance	97.4				
Acacia nigrescens	Intercept	− 6.49	0.5	− 12.9	15	<0.0001
	Cone	− 14.5	1120	− 0.013	32	0.99
	Off mound	− 0.122	0.627	− 0.195	12	0.85
	Inactive	0.594	0.534	1.11	36	0.27
	Residual deviance	122				
Ximenia americana	Intercept	− 25.1	3270	− 0.008	15	0.99
	Cone	3.06	3760	0.001	32	1
	Off mound	19.5	3270	0.006	12	1
	Inactive	18.1	3270	0.006	36	1
	Residual deviance	112				

* The area of each plot was included as an offset factor. GLMs had Poisson error distribution and a logit link function applied in the GLM MASS package of R software, with pediment as a standard among the explanatory variables in the factor class; pediment is indicated in column 2 as "intercept".

Table 5. List and proportion of visited numbers of birds at *Salvadora persica*

Common name	Scientific name	%
Wattled Staling	*Creatophora cinerea**	68.7
Burchell's Starling	*Lamprotornis australis**	12.6
Lesser Masked Weaver	*Ploceus intermedius**	8.0
Red Faced Mouse-bird	*Urocolius indicus**	6.5
Dove spp.	*Dove* spp.	1.0
Arrow Marked Babbler	*Turdoides jardineii**	0.4
African Grey Horbill	*Tockus nasutus**	0.3
Garden Warbler	*Sylvia borin**	0.3
Cape Glossy Starling	*Lamprotornis nitens*	0.2
Dark Capped Bulbul	*Pycnonotus tricolor**	0.2
Laughing Dove	*Streptopelia senegalensis*	0.2
Red billed Quelea	*Quelea quelea*	0.2
Bradfields Hornbill	*Tockus bradfieldi**	0.2
African Red-eyed bulbul	*Pycnonotus nigricans**	0.1
Blue Waxbill	*Uraeginthus angolensis*	0.1
Cape Turtle Dove	*Streptopelia capicola*	0.1
White-bellied Sunbird	*Cinnyris talatala*	0.1
African morning dove	*Streptopelia decipiens**	−
Grey Go away bird	*Corythaixoides concolor**	−
Black Headed Oriole	*Oriolus larvatus*	−
Violet-backed starling	*Cinnyricinclus leucogaster**	−
Unknown species		0.7
Total number of observed birds		2616

Asterisks indicate that the feeding behaviour of the species was observed.
“−” shows the proportion less than 0.1%

because they were most likely present before the mounds had been built. In other words, the termites built mounds up around the trees, which became half-buried in the soil. In addition, germination and establishment should be examined as processes after seed dispersal. Although some trees were established on the cones of active mounds, the cones have greater soil hardness and consequently suppress the establishment of woody plants (Yamashina 2013). Therefore, particular plant traits, such as the dynamics of root system development and germination, might explain plant preferences for mounds as habitat. In addition, the nutrient properties of termite mounds might contribute to development of characteristic vegetation. The succulent plants *S. pearsonii*, *A.zebrina* (Table 2) and *E. ingens* (Table 4) were restricted to termite mounds, and it was suggested that succulent plants are strongly associated with high soil nutrient levels in arid regions (Knight et al.1989). These are the topics that should be subjected to investigation in future studies.

This study also suggested that the species richness and abundance of woody plants increased in the order of conical parts, pediments of active mounds and inactive mounds (Table 1). Therefore, trees established on mounds might attract other animals and result in enlargement of the mounds and an increase in vegetation diversity. McCarthy et al. (1998) suggested that mammals and birds are attracted to mounds when searching for food and shelter. The faeces and urine of these animals provide plant nutrients to the soil and to seeds that have been brought by the animals, both of which contribute to the development of diverse vegetation on the mounds. In other areas, vegetation on the mounds is revealed to provide focal feeding sites for populations of large herbivores (Holdo and McDowell 2004, Loveridge and Moe 2004, Mobæk et al. 2005) and to contribute to the diversity of small mammals (Okullo et al. 2013). At the study site, the leaves of *S. persica* and *C. tomentosa* were important resources for herbivores, especially during dry seasons, since these species bear leaves year-round. Therefore, positive feedback mechanisms may exist between the encroachment and development of vegetation on termite mounds and the utilisation of these mounds by animals. Two samples of woody plant distribution also demonstrated the restricted distribution of bird-dispersed species (*i.e. S. persica* and *C. glandulosa*) on active mounds (Fig. 3A),

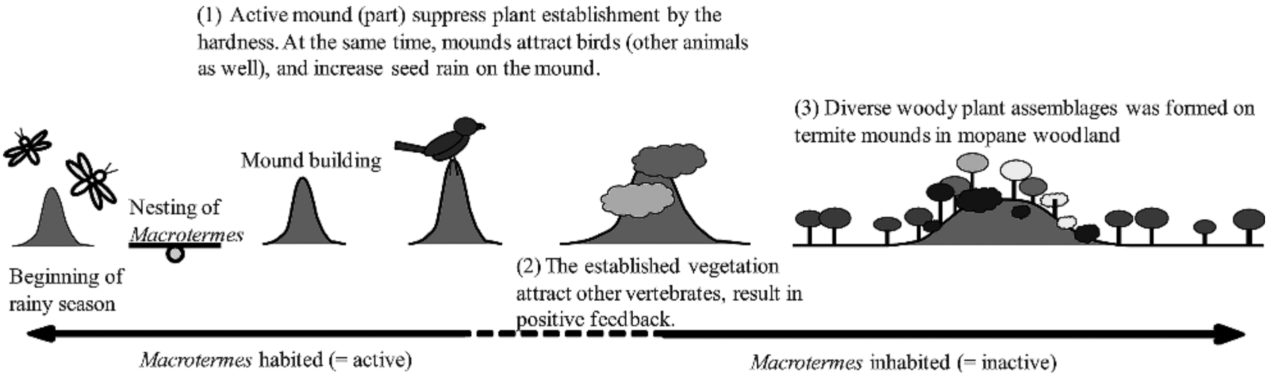

Fig. 5. Development process of a vegetated mound.

while a variety of woody plants appeared on and around inactive mounds (Fig. 3B) with a dominant tree (*C. mopane*) always widely distributed outside both the active and inactive mounds. The results of this study suggest that birds and other animals contribute to the formation of unique woody assemblages on mounds, but that the mound sampling method should be revised for future research; *i.e.* the distance between mounds was dozens of meters, so spatial autocorrelation might affect this vegetation pattern.

Hypothetical scenario for the development of termite mound vegetation

In conclusion, the following theoretical explanatory scenario for the development of mound vegetation is suggested (Fig. 5). First, *S. persica* trees are preferentially dispersed to mounds by their vectors, which use them as perching or mating sites. Some of the dispersed seeds of plants with traits that are adaptive for conditions on mounds may germinate and establish. Plants that establish subsequently attract more animals to the mounds and these positive feedback mechanisms contribute to the formation of a diverse vegetation structure. This hypothesis should be subjected to empirical testing; the outcome of such an experimental analysis will surely contribute to a better understanding of savanna vegetation ecology.

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